Check List the journal of biodiversity data

NOTES ON GEOGRAPHIC DISTRIBUTION

Check List 13 (5): 671–681
https://doi.org/10.15560/13.5.671

PENSOFT

# Unveiling the geographic distribution of *Boana pugnax* (Schmidt, 1857) (Anura, Hylidae) in Venezuela: new state records, range extension, and potential distribution

Moisés Escalona,[1, 2] David A. Prieto-Torres,[3, 4] Fernando J. M. Rojas-Runjaic[1, 5]

**1** Laboratório de Sistemática de Vertebrados, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre 90619-900, Brasil. **2** Departamento de Biología, Facultad de Ciencias, Universidad de Los Andes, Mérida 5101, Venezuela. **3** Eje BioCiencias, Centro de Modelado Científico de la Universidad del Zulia (CMC), Facultad Experimental de Ciencias, Universidad del Zulia, Maracaibo, Venezuela. **4** Red de Biología Evolutiva, Laboratorio de Bioclimatología, Instituto de Ecología, A.C., carretera antigua a Coatepec No. 351, El Haya, 91070 Xalapa, Veracruz, México. **5** Museo de Historia Natural La Salle, Fundación La Salle de Ciencias Naturales, Apartado Postal 1930, Caracas 1010-A, Venezuela.
**Corresponding author:** Moisés Escalona, moises.escalona@gmail.com

**Abstract**
*Boana pugnax* is a treefrog inhabiting open lowlands from southern Central America and northwestern South America. Its geographic distribution in Venezuela is poorly understood due, in part, its morphological similarity with *B. xerophylla* (with which is frequently confused) and the few localities documented. In order to increase the knowledge of the distribution of *B. pugnax* in the country, we examined the specimens of *B. pugnax* and *B. xerophylla* deposited in 4 Venezuelan museums, compiled the locality records of *B. pugnax*, and generated a model of potential distribution for species. We report 46 new localities for the species in Venezuela, including 8 new state records, which increases considerably its range extension.

**Key words**
Rana platanera; Chiriqui-flusse treefrog; *Boana faber* species group; Neotropics; species distribution modeling.

**Academic editor:** Rodrigo Lingnau | Received 25 January 2017 | Accepted 1 August 2017 | Published 27 October 2017

**Citation:** Escalona M, Prieto-Torres DA, Rojas-Runjaic FJM (2017) Unveiling the geographic distribution of *Boana pugnax* (Schmidt, 1857) (Anura, Hylidae) in Venezuela: new state records, range extension, and potential distribution. Check List 13 (5): 671–681. https://doi.org/10.15560/13.5.671

## Introduction

*Boana pugnax* (Schmidt, 1857) is a nocturnal, medium-sized treefrog, inhabiting in open lowlands of southern Central America and northern South America (Frost 2017). Its type locality is "along the Chiriquí rivers not far from Bocas del Toro" (Panama) according Kluge (1979). This species has a discontinuous pattern of geographic distribution, ranging from central Panama, with a hiatus in eastern Panama and western Colombia, and continuing through northwestern Colombia to northwestern Venezuela (Kluge 1979, La Marca 1996, Mijares-Urrutia and Arends 1999, Duellman 2001, Lynch and Suárez-Mayorga 2001, La Marca et al. 2010), between 5 and 540 m above sea level (a.s.l.) (Lynch and Suárez-Mayorga 2001).

*Boana pugnax* was resurrected from the synonymy of *B. crepitans* (Wied-Neuwied, 1824) by Kluge (1979), and both species were proposed as members of *B. faber* group (Faivovich et al. 2005). Recently, Orrico et al. (2017)

resurrected *B. xerophylla* (Duméril & Bibron, 1841) from the synonymy with *B. crepitans*. They defined as *Boana xerophylla* all the populations previously referred as *B. crepitans* from eastern Panama, Colombia, Venezuela, the Guianas, and northwestern Brazil. *Boana pugnax* and *B. xerophylla* are found in sympatry in some localities in Central America and northern South America (Kluge 1979, Lynch and Suárez-Mayorga 2001), and they are frequently confused due its morphological similarities (La Marca 1996), particularly when are preserved. Consequently, numerous specimens of *B. pugnax* deposited in Venezuelan museums have been previously misidentified, and the current knowledge about its geographic distribution is limited.

In Venezuela, *B. pugnax* was recorded for first time by La Marca (1996), based on a single specimen (ULABG 3292) from south of Maracaibo Lake Basin (Mérida state). Subsequently, Mijares-Urrutia and Arends (1999) documented a new locality for this species in Falcón state, northern Venezuela, and Chacón-Ortiz et al. (2004) referred it from Táchira state in the eastern piedmont of the Andes (Orinoco basin). The species also was referred by Barrio-Amorós (2004) for the Venezuelan Llanos, but neither precise locality nor voucher specimens were mentioned. Tárano (2010) described the vocalizations of *B. pugnax* from Guárico state in the Central Llanos from Venezuela, and recently Infante-Rivero and Velozo (2015) recorded this species for the Zulia state, at west Lake Maracaibo. Here we aimed to increase the knowledge about the geographic distribution of *B. pugnax* in Venezuela. After a review of 4 Venezuelan museums, we report new state records and distribution extensions for *B. pugnax* in the country. Additionally, we developed a species distribution model, in order to increase the knowledge of the distribution of this species, as well as identify gaps in the potential distribution.

## Methods

Venezuelan records of *B. pugnax* were obtained from the following Venezuelan museums: Colección de Anfibios del Laboratorio de Biogeografía de la Universidad de Los Andes (ULABG), Mérida; Colección de Vertebrados de la Universidad de Los Andes (CVULA), Mérida; Museo de Ciencias Naturales de Guanare (MCNG), Guanare; and Museo de Historia Natural La Salle (MHNLS), Caracas. We verified the identity of all specimens of MHNLS identified as *B. pugnax*, *B. xerophylla* (previously *B. crepitans,*) and *Boana* sp., and all specimens identified as *B. xerophylla* and *B. pugnax* in the other 3 collections, in order to detect specimens of *B. pugnax* yet unidentified or misidentified, and to recover as many records as possible.

We followed the morphological definition and diagnosis established by Kluge (1979), and Duellman (2001) to identify the specimens as *B. pugnax*. According these authors and Orrico et al. (2017), adult males of *B. pugnax* are larger than *B. xerophylla* [68.9–77.9 mm vs 42.9–63.8 mm of snout-to-vent length (SVL), respectively]. Further, the former species has less pigmentation in the anterior half of palpebral membrane, has darker and thicker bars on the pleural region, and dark bars on the anteroventral surface of thighs (Fig. 2). We also considered the differences in throat pigmentation noted by La Marca (1996) between *B. xerophylla* and *B. pugnax* from western Venezuela: unpigmented in *B. xerophylla* and blackish-brown colored in *B. pugnax* (Fig. 2). These morphological definitions are congruent with molecular (DNA sequences) and acoustic (advertisement calls) evidences obtained previously with specimens from western Venezuela (M. Escalona et al., unpublished data).

We generated the species distribution model (SDM) for *B. pugnax* based on all the locality records from Venezuela obtained from the museums listed above and from literature (La Marca 1996, Mijares-Urrutia and Arends 1999, Chacón-Ortiz et al. 2004, Tárano 2010), whereas those from Panama and Colombia were compiled from the Círculo Herpetológico de Panama's webpage (Círculo Herpetológico de Panamá 2017), Batrachia online database (Acosta-Galvis 2017), and literature (Kluge 1979, Lynch and Suárez-Mayorga 2001, Armesto et al. 2009, Mendez-Narvaez et al. 2014, Guarnizo et al. 2015). We did not include the records of GBIF due to difficulty of verifying the identity of specimens on which those records are based and we presumed the occurrence of an important number of misidentifications (see below). Each locality was verified and georeferenced (when necessary) using Google Earth®. All geographic coordinates were transformed in decimal degrees, based on the WGS 84 datum.

We performed the SDM under the Maximum Entropy algorithm in MaxEnt version 3.3.3k (Phillips et al. 2006) due to its better proved performance, including a lower commission error (i.e., overestimating) in the models (e.g., Elith et al. 2006, 2011, Peterson et al. 2007). We used interpolated climate data from WorldClim project (Hijmans et al. 2005) and the terrestrial ecoregions (Olson et al. 2001), both at 30″ resolution (~1 km$^2$ cell size), as input variables in order to characterize the ecological niche and potential distribution of the focal species. Bioclimatic layers were cropped to include latitudes 01.1947° N to 12.4193° N and longitudes 089.8861° W to 059.9454° W. Despite the fact that categorical variables, such as ecoregions or ecosystems are not commonly used in SDM studies, we decided to include it because this predictor may be considered as variable related directly with the ecology of the focal species (Pearson and Dawson 2003, Austin 2007, Rödder et al. 2009, Jiménez-Valverde et al. 2011). Thus, the obtained models provide a first approximation indicating the better hypotheses for the potential distribution of *B. pugnax* at the current time.

We used a geographical clip (Fig. 1) based on the intersection of Terrestrial Ecoregions (Olson et al. 2001) and the Biogeographical Provinces of the Neotropic (Morrone 2014) in order to create an area for model calibration (or M sensu BAM diagram; see Soberón and Peterson 2005, Barve et al. 2011). In addition, for a first

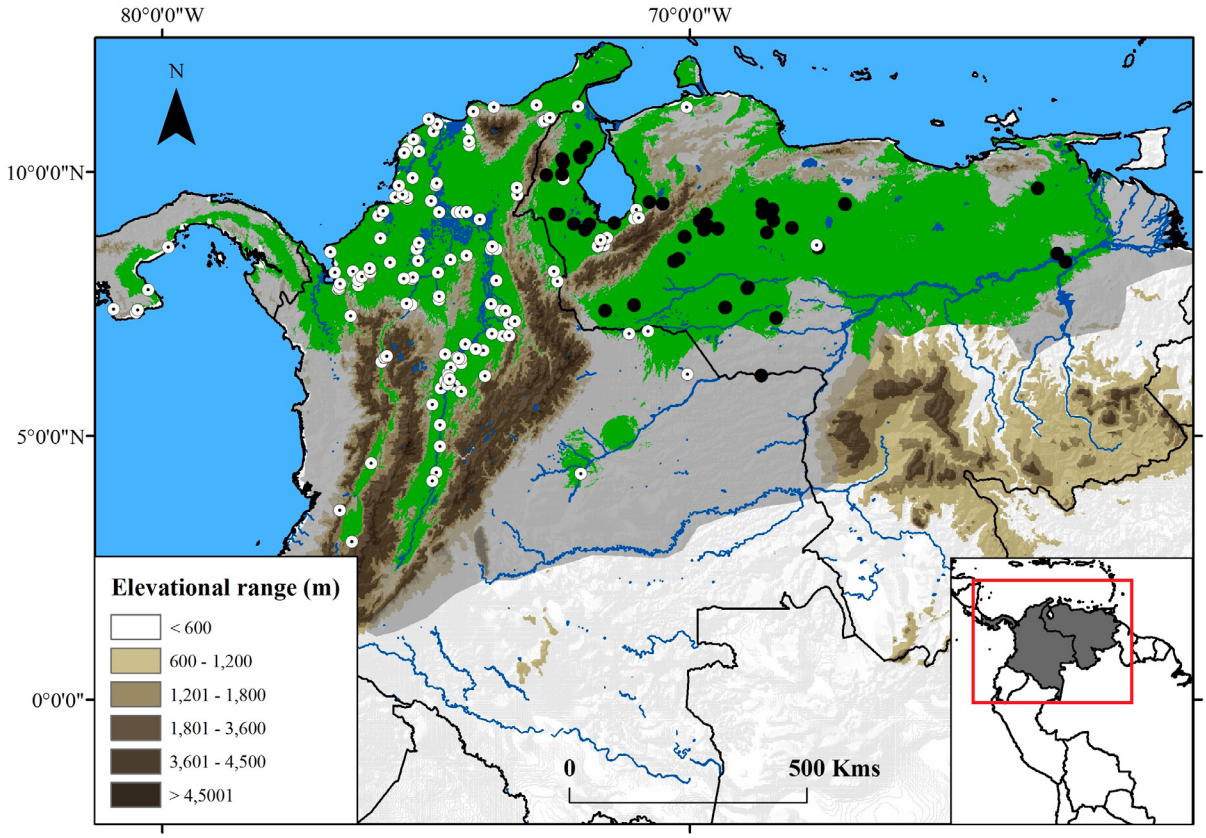


**Figure 1.** Species distribution model (SDM) and locality records of *Boana pugnax*. White-with-black-dot circles: literature records from Kluge (1979), La Marca (1996), Lynch and Suárez-Mayorga (2001), Armesto et al. (2009), Tárano (2010), and Guarnizo et al. (2015). Black circles: new records based on museum data. Gray area: calibration area (see Soberón and Peterson 2005, Barve et al. 2011) used in the SDM reconstruction. Green area: Potential SDM with the threshold value of Fixed Omission Value 5 (FOV5).

explorative analysis, we used the 20 bioclimate layers and assessed which variables were the most important for the model, according to the Jackknife test calculated in MaxEnt (Berger 2007, Elith et al. 2011). In a second modelling exercise, we generated the species distribution using non-correlated environmental variables ($r < 0.8$) in combination with the most relevant environmental variables identified in the first approach (e.g., Ortega-Andrade et al. 2015). These additional steps allowed us to reduce the collinearity of variables and over-fitting of the generated distribution models (see Peterson et al. 2011).

The SDM was generated with 80% of the locality records (training data) while the other 20% was used for model evaluation (testing data). We ran 1,000 iterations, with no extrapolation in order to avoid artificial projections of the extreme values of the ecological variables (Elith et al. 2011, Stohlgren et al. 2011). All other parameters in MaxEnt were maintained as default settings. We ran 10 cross-validate replicates to calculate confidence intervals in order to select the best model based on the performance of area under the curve or "AUC" (Elith et al. 2006, 2011).

Then, we used the logistic response to obtain the values for habitat suitability (continuous probability from 0 to 1; Phillips et al. 2006), which were subsequently converted to binary presence-absence values on the basis of the established threshold value, defined herein as the "Fixed Omission Value 5" or FOV5 (Liu et al. 2013). This threshold allowed us to evaluate the species' distribution by minimizing commission errors (i.e., over-predictions) in our final binary maps. Finally, the performance of the selected model was assessed based the commission and omission errors (Anderson et al. 2003) and by applying the Partial-ROC (Receiver Operating Characteristic) curves test (Lobo et al. 2008, Peterson et al. 2008). This criterion was used to solve problems associated with an inappropriate weighting of the omission and commission errors during the AUC analysis (see Lobo et al. 2008, Peterson et al. 2008).

## Results

Our study includes new information about the *B. pugnax*'s distribution, with 179 unique occurrences recorded (57 points from Venezuela, 117 from Colombia, and 5 from Panama), including localities quite outside from the recognized geographic distribution range (Fig. 1, Table 1, Table A1). Surprisingly, we found an important number of misidentifications in the Venezuelan museums reviewed (ca 79%). A total of 46 new localities were recorded for first time for Venezuela, extending the geographic distribution of *B. pugnax* ca 852 km east of the closest know locality in the country (Fig. 1, Table 1).

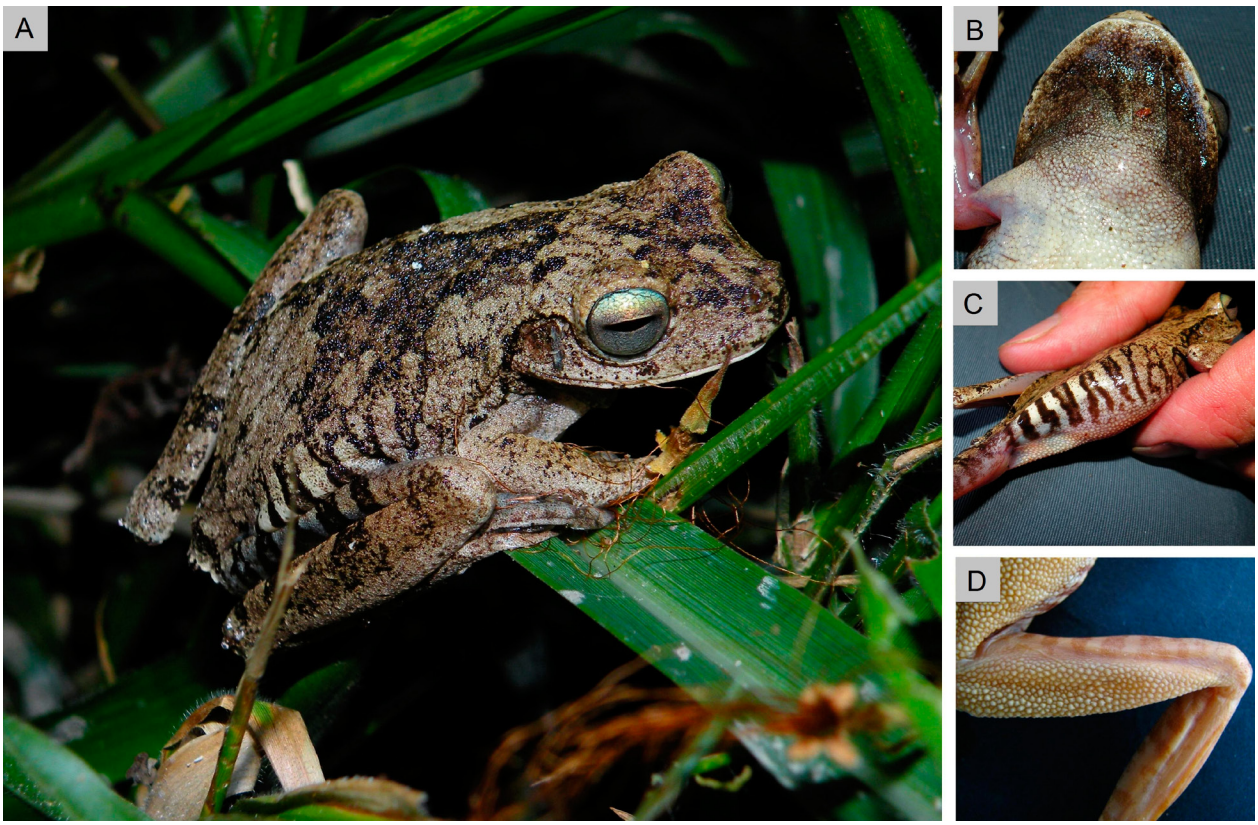


**Figure 2.** *Boana pugnax* adult male in life (ULABG 7739) from Caño San Mateo (South of Maracaibo Lake Basin, Mérida state, Venezuela). **A.** Dorsolateral view. **B.** Ventral view showing the blackish coloration at throat level. **C.** Color pattern of the flank of body. **D**. Ventral view at thigh, showing its color pattern in preservative. Photos: Ivan Mendoza (A–C) and Moisés Escalona (D).

## Discussion

The new occurrences, based on confirmed identification of specimens, include new state records for Apure, Anzoátegui, Barinas, Cojedes, Guárico, Monagas, Portuguesa, and Trujillo. Thus, our new records change considerably the previous statement of *B. pugnax* as restricted to western Venezuela (Duellman 2001, Lynch and Suárez-Mayorga 2001, Chacón-Ortiz et al. 2004, La Marca et al. 2010), and exceed the prediction formulated by La Marca et al. (2010), who suggested that this species was expected to be in Apure, Barinas, and Zulia state.

All the 116 specimens recorded (representing 57 unique localities) for *B. pugnax* in Venezuela are between 0–605 m a.s.l. (Table 1, Appendix Table A1). These records reduce scarcely the elevational range reported previously for Venezuela (0–700 m a.s.l.) by Barrio-Amorós (2004). Other localities documented in Panama are below 100 m a.s.l. (Duellman 2001), while in Colombia are mainly below 500 m a.s.l. (Lynch and Suárez-Mayorga 2001). Thus, this species seems be predominantly from lowlands as suggested Kluge (1979) and Lynch and Suárez-Mayorga (2001). In this sense, it is important to note that our model did not predict 4 localities reported with higher elevation in Colombia (see Table A1): Bitaco, Valle del Cauca, at 1426 m a.s.l. (voucher USNM 151982 [USNM database]); Minca, Magdalena, at 1530 m a.s.l. (Lynch and Suárez-Mayorga 2001); one locality from the Valle del Cuaca, at 940 m a.s.l. and another locality from the Cauca, at 1200 m a.s.l. (Mendez-Narvaez et al. 2014). Despite that we argue the need of validation at field for model in these areas, an alternative explanation for these results may involve the misidentifications for the specimens as we found in the Venezuelan museums (see above).

The predictive potential SDM of *B. pugnax* had a high success-rate for the AUC-test (0.889) and ROC-Partial (1.24 ± 0.22) values, as well as low omission error (17.64%; $N = 7$) for the threshold values (0.103). Thus, the SDM was considered to be statistically significant (Peterson et al. 2008, Elith et al. 2011). The variables that contributed most to the model were mean temperature of coldest quarter (28.7%), mean temperature of wettest quarter (17.7%), temperature seasonality (15.0%), precipitation of wettest quarter (14.2.1%), and isothermality (8.7%); which comprised 84.3% of the contribution for the estimation model (Table 2).

Interestingly, the most important variable found here (i.e. mean temperature of coldest quarter) support the Lynch and Suárez-Mayorga (2001) affirmation that *B. pugnax* may be "... unable to breed in cooler environments…". The *B. pugnax* distribution range (according the FOV5) totalled ~658,400 km$^2$ along the region from Venezuela to Panama, with ~394,300 km$^2$ (59.9%) estimated for Venezuela, ~245,400 km$^2$ (37.3%) for Colombia, and only ~18,700 km$^2$ (2.8%) for Panama (Fig. 1). These values were greater than previously thought (La Marca et al. 2010). Lynch and Suárez-Mayorga (2001)

**Table 1.** New state locality records of *Boana pugnax* in Venezuela. Geographic coordinates are provided based on the WGS 84 datum. Source: Colección de Vertebrados de la Universidad de Los Andes (CVULA), Mérida; Museo de Ciencias Naturales de Guanare at Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamora (MCNG), Guanare; Museo de Historia Natural La Salle (MHNLS), Caracas; and the Colección de Anfibios y Reptiles del Laboratorio de Biogeografía de la Universidad de Los Andes (ULABG), Mérida. Abbreviation: a.s.l. = above sea level.

| No. | State: locality | Latitude, longitude | Elevation a.s.l. (m) | Source (voucher) |
|---|---|---|---|---|
| 1 | Anzoátegui: Mamo | 08.4608, –063.0350 | 75 | MHNLS (8701–8707, 8820) |
| 2 | Anzoátegui: Sector Punta Cuchillo, around Caimán lagoon, NE Orinoquia bridge, north edge of río Orinoco | 08.2933, –062.8824 | 2 | MNHLS (20267) |
| 3 | Apure: Modulo Fernando Corrales | 07.2333, –068.3666 | 59 | CVULA (3416, 3417); MCNG (168, 169, 647, 651) |
| 4 | Apure: Hato El Frío | 07.8166, –068.8958 | 54 | MHNLS (7466, 8619–8624, 16315); ULABG (5446) |
| 5 | Apure: Paso El Burro | 07.3749, –071.6048 | 199 | CVULA (7078) |
| 6 | Apure: Hato El Cedral, field near Matiyure camp | 07.4298, –069.3250 | 83 | ULABG (7781–7783, 7790–7792) |
| 7 | Apure: Caño Negro, 6 km SW Buena Vista | 06.1416, –068.6433 | 59 | MHLS (8979–8981) |
| 8 | Apure: La Ramera road, Las Ventanas, Hato El Frío | 07.8011, –068.9141 | 54 | MHNLS (12112) |
| 9 | Apure: Hato El Cedral | 07.4350, –069.3261 | 83 | MHNLS (14283, 14792) |
| 10 | Apure: Laguna de Derbio, near Hato El Frío's biological station | 07.8166, –068.8958 | 54 | MHNLS (16269–16272) |
| 11 | Barinas: 40 km S Barinas | 08.3567, –070.2095 | 133 | CVULA (502) |
| 12 | Barinas: El Irel, Barrancas | 08.7715, –070.0976 | 237 | CVULA (2541, 2544, 2551, 2553, 6919); ULABG (5594, 5666, 5668, 6970) |
| 13 | Barinas: Reserva Forestal Caparo, experimental station | 07.4715, –071.0548 | 139 | ULABG (5594) |
| 14 | Barinas: Sector El Moraleño | 08.3047, –070.2939 | 141 | MHNLS (21245, 21246) |
| 15 | Cojedes: Río Portuguesa, 15 km El Baúl | 08.8522, –068.5416 | 47 | MHNLS (1942, 1943, 1945–1947) |
| 16 | Cojedes: Hato El Tirado | 09.0800, –068.4133 | 74 | MHNLS (6312, 6313, 6323–6325) |
| 17 | Cojedes: El Veladero, 100 m SE Las Vegas | 09.3833, –068.6333 | 85 | MHNLS (6423–6426) |
| 18 | Cojedes: Hato Itabana, 38 km SW Las Vegas | 09.2333, –068.4666 | 77 | MHNLS (6462) |
| 19 | Cojedes: Hato Los Caballos, 38 km S Tinaco | 09.2933, –068.4305 | 89 | MHNLS (6991–6994) |
| 20 | Cojedes: Hato Piñero | 08.9380, –068.0669 | 112 | MHNLS (12365) |
| 21 | Cojedes: Campus Fundación La Salle (FLASA), San Carlos | 09.2205, –068.6238 | 77 | MHNLS (13830) |
| 22 | Guárico: El Sombrero | 09.3872, –067.0533 | 147 | MHNLS (2896) |
| 23 | Guárico: Fundo Pecuario Masaguaral | 08.5666, –067.5833 | 72 | Tárano 2010 |
| 24 | Guárico: Hato Masaguaral | 08.5644, –067.5644 | 72 | MHNLS (14102) |
| 25 | Monagas: Hato La Candelaria, 30 km Maturín | 09.6888, –063.4083 | 82 | MHNLS (2945, 2946) |
| 26 | Portuguesa: Fundaguanare, Guanare | 09.0537, –069.7324 | 148 | MCNG (627) |
| 27 | Portuguesa: Mesa de Cavaca | 09.0762, –069.8150 | 285 | MCNG (638) |
| 28 | Portuguesa: Fundo El Drago | 08.9281, –069.4710 | 98 | MCNG (801–803) |
| 29 | Portuguesa: Río Tucupido | 08.9076, –069.7283 | 122 | MCNG (809) |
| 30 | Portuguesa: El Potrero, way to Suruguapo, aprox. 12 km old road Guanare-Acarigua | 09.1981, –069.6865 | 202 | ULABG (5367) |
| 31 | Portuguesa: Road Guanare-Guanarito, 8 km intersection road Guanare-Barquisimeto | 08.9769, –069.6562 | 128 | ULABG (7749, 7750) |
| 32 | Trujillo: Sabana de Mendoza | 09.4369, –070.7663 | 166 | MHNLS (2955) |
| 33 | Trujillo: Between Valera and Trujillo, near fuel station | 09.3977, –070.5171 | 396 | ULABG (5704, 5705) |
| 34 | Zulia: Santa Bárbara del Zulia | 09.0024, –071.8891 | 9 | CVULA (968, 969, 971, 972, 974, 3745, 4531, 4552, 4824) |
| 35 | Zulia: Santa Bárbara del Zulia, Malariología's house | 09.0083, –071.9050 | 7 | MHNLS (14710) |
| 36 | Zulia: Santa Cruz del Zulia | 08.9070, –071.9854 | 10 | CVULA (969, 970) |
| 37 | Zulia: El Pino | 09.0347, –071.4304 | 21 | ULABG (2530, 2531, 2989, 2991) |
| 38 | Zulia: Hacienda La Esperanza (La Universidad del Zulia), km 107 road Maracaibo-Machiques | 10.1863, –072.3983 | 108 | CVULA (3665) |
| 39 | Zulia: Río Yasa | 09.9430, –072.7230 | 156 | MHNLS (1580, 2966) |
| 40 | Zulia: Hato Los Mangos, Machiques | 10.2500, –072.4175 | 123 | MHNLS (9622) |
| 41 | Zulia: Caño Caimán, 7 km N Encontrados | 09.0200, –072.1939 | 19 | MHNLS (15744–15747) |
| 42 | Zulia: Hacienda Grano de Oro, remanent forest, Campo Boscán | 10.2711, –072.0683 | 2 | MHNLS (16866, 16870–16873) |
| 43 | Zulia: Hacienda Grano de Oro, Campo Boscán | 10.4649, –071.9541 | 96 | MHNLS (18602) |
| 44 | Zulia: Hacienda Cincelejo, Campo Boscán | 10.3230, –072.0891 | 9 | MHNLS (16889, 16890, 16902) |
| 45 | Zulia: Hacienda San Martín, Sector Aguas Negras (ancient Juan Manuel's house) | 09.1872, –072.4783 | 31 | MHNLS (17946, 17947, 17989, 17990) |
| 46 | Zulia: Hacienda Monterrey, Sector Calle Larga | 09.9560, –072.4192 | 104 | MHNLS (20330–20333) |

**Table 2.** Summary of the selected, not-correlated, environmental variables with relative contributions (%) to the potential distribution model of *Boana pugnax* using MaxEnt 3.3.3k.

| Abbreviation | Environmental variable | Percentage of contribution |
|---|---|---|
| Bio 11 | Mean temperature of coldest quarter | 28.7 |
| Bio 08 | Mean temperature of wettest quarter | 17.7 |
| Bio 04 | Temperature seasonality (standard deviation *100) | 15.0 |
| Bio 16 | Precipitation of wettest quarter | 14.2 |
| Bio 03 | Isothermality (bio2/bio7) (* 100) | 8.7 |
| Biome | Terrestrial ecoregions | 4.7 |
| Bio 19 | Precipitation of coldest quarter | 3.4 |
| Bio 17 | Precipitation of driest quarter | 3.0 |
| Bio 07 | Temperature annual range (BIO5–BIO6) | 2.4 |
| Bio 09 | Mean temperature of driest quarter | 2.2 |

mentioned that *B. pugnax* was a near-Colombian endemic species; however, our results suggest that this taxon is more extensively distributed in Venezuela.

Our SDM predicts the presence of *B. pugnax* in 14 ecosystems (Olson et al. 2001) for Venezuela; 4 of them encompass ~90% of its total area estimated in the country. The most extensive ecosystems were the savannah (~190,250 km$^2$; 48.25% of the extent areas), the dry forests (~84,500 km$^2$; 21.44%), the xeric shrublands forests (~63,000 km$^2$; 15.99%), and the Catatumbo moist forests (15,600 km$^2$; 3.96%). It is important to note that our SDM suggests the presence of *B. pugnax* in additional ecosystems (including moist forests, montane forests, mangroves, wetlands, and swamp) throughout Venezuelan states: Lara, Carabobo, Miranda, Sucre, and Bolívar. All these predictions will need a validation at field. However, the presence in these regions is expected on the base of habitat type and continuity reported in the areas, which is congruent with the species' biology (La Marca et al. 2010).

Additionally, the SDM suggest lowest suitability values throughout the Cordillera de Mérida, the Cordillera Oriental (Eastern Andes in Colombia), and the Sierra de Perijá (northern border between Venezuela and Colombia), which could be interpreted as potential geographic and ecological barriers for the dispersion of *B. pugnax* (Fig. 1). Hence, the change of physical variables along the elevational gradient in these mountains could constrain the spread of individuals through them (Janzen 1967). This is congruent with the allozymatic differences found between populations from northwest and southeast of Cordillera de Mérida (Nava 2005). However, the current evidence let us to treat all populations of *B. pugnax* as a single species. Nevertheless, these disjunct populations could merit the recognition as Evolutionarily Significant Units (ESUs) in the future, which will be important in a biology conservation context (Moritz 1994).

Finally, our results encourage the need to continue studying the biology of *Boana pugnax*, providing an ecological framework of where to focus the future survey efforts in Venezuela, as well as in Colombia and Panama. Modeled distributions have the advantage of filling gaps that point-based distributions present as a result of the necessarily incomplete sampling (Peterson 2001, Mota-Vargas and Rojas-Soto 2012), but at same time identify the most important variables for the species persistence (Soberón and Peterson 2005, Elith et al. 2011). Furthermore, this technique provides better results in terms of spatial and numerical sensitivity as well as lower values of omission and a moderate extent of predicted areas; therefore, are widely used in ecology, evolution, conservation, and management (e.g., Soberón and Peterson 2005, Mota-Vargas and Rojas-Soto 2012, Ortega-Andrade et al. 2015). Additionally, this study illustrates the importance of the museums specimens as a source of data (see Rocha et al. 2014) to increase the knowledge about species' geographic distribution.

## Acknowledgements

We would like to acknowledge the contributions of the following individuals and institutions: Pedro Cabello and Ygrein Roos, for their the assistance in the re-identification of the specimens of MHNLS, and Enrique La Marca (ULABG), Amelia Díaz de Pascual (CVULA), and Juan Elías García-Pérez (MCNG), for support during the visit to their respective institutions. ME and FRR are benefited with postgraduate scholarships by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; process number 1578956) and the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, process 142444/2014-6), respectively. DPT thanks La Universidad del Zulia for funding and logistical support (CONDES project no. 0247-13), as well as to Consejo Nacional de Ciencia y Tecnología (CONACyT, Mexico) for the doctoral scholarship.

## Authors' Contributions

ME and FRR identified the specimens and compiled the database of records; DPT performed the species distribution model; and ME, DPT, and FRR wrote the manuscript.

## References

Acosta-Galvis AR, Alfaro Vejarano JP (2011) Anfibios del Casanare. In: Usma JS, Trujillo F, Ayala LT (Eds) Biodiversidad del Casanare: Ecosistemas Estratégicos del Departamento. Gobernación de Casanare/WWF Colombia, Bogotá DC, 134–147.

Acosta-Galvis AR (2017) Lista de los Anfibios de Colombia: Referencia en línea V.07.2017.0. http://www.batrachia.com. Accessed on: 2017-02-01.

Anderson R, Lew D, Peterson A (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling 162: 211–232. https://doi.org/10.1016/s0304-3800(02)00349-6

Armesto O, Esteban JB, Torrado R (2009) Fauna de anfibios del municipio de Cúcuta, Norte de Santander, Colombia. Herpetotropicos 5: 57–63.

Austin M (2007) Species distribution models and ecological theory: a critical assessment and some possible new approaches. Ecological Modelling 200: 1–19. https://doi.org/10.1016/j.ecolmodel.2006.07.005

Barrio-Amorós CL (2004) Amphibians of Venezuela systematic list, distribution and references, an update. Revista de Ecología Latinoamericana 9: 1–48.

Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Soberón J, Villalobos F (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modelling 222: 1810–1819. https://doi.org/10.1016/j.ecolmodel.2011.02.011

Berger YG (2007) A Jackknife variance estimator for unistage stratified samples with unequal probabilities. Biometrika 94: 953–964.

Chacón-Ortiz A, Pascual AD De, Godoy F (2004) Aspectos reproductivos y desarrollo larval de *Hyla pugnax* (Anura: Hylidae) en el piedemonte andino de Venezuela. Revista de la Academia Colombiana de Ciencias 28: 391–402.

Círculo Herpetológico de Panamá (2017) Base de datos herpetológica de Panamá. http://biogeodb.stri.si.edu/chp/. Accessed on: 2017-02-01.

Duellman WE (2001) The Hylid Frogs of Middle America, 2nd edition. Society for the Study of Amphibians and Reptiles, Ithaca, New York, 1170 pp.

Elith J, Graham C, Anderson R, Dudik M, Ferrier S, Guisan A, Hijmans R, Huettmann F, Leathwick J, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton J McC M, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elith, J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17: 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Faivovich J, Haddad CFB, Garcia PCDA, Frost DR, Campbell JA,Wheeler WC (2005) Systematic review of the frog family Hylidae, with special reference to Hylinae: a phylogenetic analysis and taxonomic revision. Bulletin of the American Museum of Natural History 294: 1–240. https://doi.org/10.1206/0003-0090(2005)294[0001:srotff]2.0.co;2

Frost DR (2017) Amphibian Species of the World: an online reference. Version 6.0. Electronic Database. American Museum of Natural History, New York, USA. http://research.amnh.org/herpetology/amphibia/index.html. Accessed on: 2017-07-01.

Graham CH, Elith J, Hijmans RJ, Guisan A, Peterson AT, Loiselle BA (2008) The influence of spatial errors in species occurrence data used in distribution models. Journal of Applied Ecology 45: 239–247. https://doi.org/10.1111/j.1365-2664.2007.01408.x

Guarnizo CE, Paz A, Muñoz-Ortiz A, Flechas SV, Méndez-Narváez J, Crawford AJ (2015) DNA barcoding survey of anurans across the Eastern Cordillera of Colombia and the impact of the Andes on cryptic diversity. PLoS ONE 10: e0127312. https://doi.org/10.1371/journal.pone.0127312

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978. https://doi.org/10.1002/joc.1276

Infante-Rivero E, Velozo P (2015) Inventario de anfibios y reptiles en la agropecuaria San Sebastián, tierras bajas de Machíques de Perijá, estado Zulia, Venezuela. Boletín del Centro de Investigaciones Biológicas 49: 138–150.

Janzen DH (1967) Why mountain passes are higher in the tropics. The American Naturalist 101: 233–249. https://doi.org/10.1086/282487

Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. Biological Invasions 13: 2785–2797. https://doi.org/10.1007/s10530-011-9963-4

Kluge AG (1979) The gladiator frogs of Middle America and Colombia. A reevaluation of their systematics (Anura: Hylidae). Occasional Papers of the Museum of Zoology, University of Michigan 688: 1–24.

La Marca E (1996) First record of *Hyla pugnax* (Amphibia: Anura: Hylidae) in Venezuela. Bulletin Maryland Herpetological Society 32: 35–42.

La Marca E, Rueda JV, Ardila-Robayo MC, Solís F, Ibáñez R, Jaramillo C, Fuenmayor Q, Barrio CL (2010) *Hypsiboas pugnax*. The IUCN Red List of Threatened Species 2010. e.T55618A11340255. http://www.iucnredlist.org/. Accessed on: 2016-01-08.

Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography 40: 778–789. https://doi.org/10.1111/jbi.12058

Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17: 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x

Lynch JD, Suárez-Mayorga AM (2001) The distributions of the gladiator frogs (Hyla boans group) in Colombia, with comments on size variation and sympatry. Caldasia 23: 491–507.

Mendez-Narvaez J, Ortiz-Navia JO, Bolívar-G W (2014) *Hypsiboas pugnax* Schmidt, 1857 and *Scinax ruber* Laurenti, 1768 (Amphibia: Anura): Distribution extension in the Río Cauca Valley, Colombia. Check List 10: 409–410. https://doi.org/10.15560/10.2.409

Mijares-Urrutia A, Arends A (1999) Additional new regional and local records of amphibians and reptiles from the state of Falcón, Venezuela. Herpetological Review 30: 115.

Moritz C (1994) Defining 'evolutionarily significant units' for conservation. Trends in Ecology & Evolution 9: 373–375. https://doi.org/10.1016/0169-5347(94)90057-4

Morrone JJ (2014) Biogeographical regionalization of the Neotropical region. Zootaxa 3782: 1–110. https://doi.org/10.11646/zootaxa.3782.1.1

Mota-Vargas C,Rojas-Soto OR (2012) The importance of defining the geographic distribution of species for conservation: the case of the Bearded Wood-Partridge. Journal for Nature Conservation 20: 10–17. https://doi.org/10.1016/j.jnc.2011.07.002

Naimi B, Hamm NAS, Groen TA, Skidmore AK, Toxopeus AG (2013) Where is positional uncertainty a problem for species distribution modelling? Ecography 37: 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

Nava F (2005) Estudio filogeográfico de las ranas plataneras (Anura: Hylidae), en la región occidental de Venezuela, a través de electroforesis de aloenzimas. Licentiate thesis, Departamento de Biología, Universidad de Los Andes, Mérida, Venezuela, 51 pp.

Olson DM, Dinerstein E, Wikramanayake ED, et al. (2001) Terrestrial ecoregions of the world: A new map of life on earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience 51: 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Orrico VGD, Nunes I, Mattedi C, Fouquet A, Lemos AW, Rivera-Correa M, Lyra ML, Loebmann D, Pimenta BVS, Caramaschi U, Rodrigues MT, Haddad CFB (2017) Integrative taxonomy supports the existence of two distinct species within *Hypsiboas crepitans* (Anura: Hylidae). Salamandra 53: 99–113.

Ortega-Andrade HM, Prieto-Torres D, Gómez-Lora I, Lizcano D (2015) Ecological and geographical analysis of the distribution of the Mountain Tapir (*Tapirus pinchaque*) in Ecuador: importance of protected areas in future scenarios of global warming. PLoS ONE 10:e0121137. https://doi.org/10.1371/journal.pone.0121137

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Peterson AT (2001) Predicting species' geographic distributions based on ecological niche modeling. Condor 103: 599–605. https://doi.org/10.1650/0010-5422(2001)103[0599:PSGDBO]2.0.CO;2

Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecological Modelling 213: 63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Peterson AT, Papeş M, Eaton M (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30: 550–560. https://doi.org/10.1111/j.2007.0906-7590.05102.x

Peterson AT, Soberon J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araujo M (2011) Ecological Niches and Geographic Distributions. Press PU, New Jersey, USA, 328 pp.

Phillips S, Anderson R, Schapire R (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Rocha LA, Aleixo A, Allen G, et al. (2014) Specimen collection: an essential tool. Science 344(6186): 814–815. https://doi.org/10.1126/science.344.6186.814

Rödder D, Schmidtlein S, Veith M, Lötters S (2009) Alien invasive slider turtle in unpredicted habitat: a matter of niche shift or of predictors studied? PLoS ONE 4: e7843. https://doi.org/10.1371/journal.pone.0007843

Schmidt O (1857) Diagnosen neuer Frösche des zoologischen Cabinets zu Krakau. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenchaftliche Classe 24: 10–15.

Soberón J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2: 1–10. https://doi.org/10.17161/bi.v2i0.4

Stohlgren TJ, Jarnevich CS, Esaias WE, Morisette JT (2011) Bounding species distribution models. Current Zoology 57: 642–647. https://doi.org/10.1093/czoolo/57.5.642

Tárano Z (2010) Advertisement calls and calling habits of frogs from a flooded savanna of Venezuela. South American Journal of Herpetology 5: 221–240. https://doi.org/10.2994/057.005.0308

Wied-Neuwied MAP (1824) Abbildungen zur naturgeschichte brasiliens. Lyes-Industrie-Comptoir, Weimar. 612 pp. https://doi.org/10.5962/bhl.title.63798

# Appendix

**Table A1.** Records of *Boana pugnax* previously reported for Colombia (CO) and Panama (PA), and additional records for Venezuela (VE) analyzed for this study. Acronyms correspond to AMNH: American Museum of Natural History; ANDES-A: Museo de Historia Natural de la Universidad de Los Andes; ANSP: Academy of Natural Sciences; a.s.l.: above sea level; BATRACHIA: Checklist of Colombian Amphibians' webpage; Colombia; CAS: Museum of California Academy of Science; CHPW: Círculo Herpetológico de Panama's webpage; Philadelphia; CO: Colombia; FMNH: Field Museum of Natural History; UMMZ: University of Michigan Museum of Zoology; IAvH: Instituto Alexander von Humboldt; ICN: Instituto de Ciencias Naturales, Colombia; ICNMH: Museo de Historia Natural del Instituto de Ciencias Naturales, Colombia; KU: Museum of Natural History, University of Kansas; MCZ: Museum of Comparative Zoology; MBLUZ: Museo de Biología de la Universidad del Zulia; MHUA: Museo de Herpetología de la Universidad de Antioquia, Colombia; NS: National Fish and Wildlife Laboratories, University of New Mexico; PA: Panama; UIS-MHN: Universidad Industrial de Santander Museo de Historia Natural, Colombia; USNM: National Museum of Natural History (USA);USNMW: National Museum of Natural History (USA) online database; VE: Venezuela.

| Locality | State: country | Voucher | Latitude | Longitude | Elevation (m a.s.l.) | Source |
|---|---|---|---|---|---|---|
| Hotel El Lago | Antioquia: CO | MHUA (4709) | 05.8996 | –074.7233 | 281 | BATRACHIA |
| Termoelectrica La Sierra | Antioquia: CO | MHUA (0232, 3210) | 06.1913 | –074.5900 | 113 | BATRACHIA |
| Finca La Suiza | Antioquia: CO | MHUA (1832–1833, 3179) | 06.2996 | –074.5317 | 120 | BATRACHIA |
| Quebrada la Oque, Finca guarda el sol | Antioquia: CO | MHUA (7110) | 06.3996 | –075.8483 | 454 | BATRACHIA |
| 10 km antes de Sta. Fe de Antioquia | Antioquia: CO | MHUA (3223) | 06.4829 | –075.7816 | 532 | BATRACHIA |
| Puerto Berrio | Antioquia: CO | AMNH (39013, 39015, 39021–39025); UMMZ (56506) | 06.4892 | –074.4108 | 71 | Kluge (1979) |
| No locality mentioned | Antioquia: CO | MHUA (2642) | 06.5079 | –075.7483 | 696 | BATRACHIA |
| Hda. Sta. Barbara | Antioquia: CO | MHUA (675, 1565-1667, 2199, 2410, 2566, 2598, 2599, 3238, 4357, 4819, 4820) | 06.5496 | –074.6400 | 600 | BATRACHIA |
| Ciénaga Barbacoas, Finca Casa Loma | Antioquia: CO | MHUA (6444, 6393) | 06.7412 | –074.2567 | 57 | BATRACHIA |
| Finca Monteloro | Antioquia: CO | MHUA (3155) | 07.2746 | –076.4316 | 202 | BATRACHIA |
| Hacienda Las Mercedes, Bosque Quebradona | Antioquia: CO | MHUA (0093, 0580) | 07.4829 | –075.2816 | 171 | BATRACHIA |
| Rio Rayo | Antioquia: CO | MHUA (7519) | 07.5079 | –075.3733 | 154 | BATRACHIA |
| No locality mentioned | Antioquia: CO | MHUA (5699) | 07.5745 | –074.7650 | 110 | BATRACHIA |
| Finca No hay como Dios, Región Bamba | Antioquia: CO | MHUA (5528) | 07.6495 | –074.7567 | 96 | BATRACHIA |
| Estacion Tulenapa, Finca Corpoica | Antioquia: CO | MHUA (2694, 3290, 6238) | 07.7829 | –076.6732 | 85 | BATRACHIA |
| Campamento Los Almendros, Augura | Antioquia: CO | MHUA (2288) | 07.7912 | –076.6483 | 90 | BATRACHIA |
| Estación Cocorna | Antioquia: CO | MHUA (0675) | 06.0413 | –074.6400 | 151 | BATRACHIA |
| Finca La Granja | Antioquia: CO | MHUA (2303) | 07.8162 | –076.6566 | 88 | BATRACHIA |
| Parque Recreativo Camacol | Antioquia: CO | MHUA (3639) | 07.8829 | –076.6316 | 64 | BATRACHIA |
| Hacienda La Candelaria | Antioquia: CO | MHUA (0038, 1279, 1557) | 07.9745 | –075.2733 | 83 | BATRACHIA |
| Vía Caucasia Nechi; Hacienda. La Leyenda | Antioquia: CO | MHUA (1558, 2516, 6031, 6032, 2279, 2336) | 08.0079 | –075.2483 | 85 | BATRACHIA |
| Nechi | Antioquia: CO | FMNH (54778–54782) | 08.0944 | –074.7761 | 29 | Kluge (1979) |
| Turbo | Antioquia: CO | Uncatalogued | 08.0947 | –076.7283 | 0 | Lynch & Suárez-Mayorga (2001) |
| Alto de Quimari | Antioquia: CO | FMNH (61751) | 08.1167 | –076.3833 | 411 | Kluge (1979) |
| Primera alternativa para el puerto, entre el rio Necocli y la casa del topógrafo | Antioquia: CO | MHUA (7863) | 08.4831 | –076.8103 | 2 | BATRACHIA |

*Continued*

**Appendix, Table A1.** *Continued.*

| Locality | State: country | Voucher | Latitude | Longitude | Elevation (m a.s.l.) | Source |
|---|---|---|---|---|---|---|
| Caño Limón, Asoc. Cravo Norte, landfill | Arauca: CO | ICN (27699, 27806, 27807) | 06.9378 | –071.1525 | 130 | Lynch & Suárez-Mayorga (2001) |
| Arauca, Hato el Venero's house | Arauca: CO | IAvH (444, 2503, 2504, 2982, 3697–3700, 3902, 3905) | 06.9794 | –070.7981 | 123 | Lynch & Suárez-Mayorga (2001) |
| Piscicultura Soplaviento | Atlántico: CO | IAvH (582, 586) | 10.3914 | –075.1356 | 11 | Lynch & Suárez-Mayorga (2001) |
| Los Pendales | Atlántico: CO | USNM (152142) | 10.6167 | –075.2167 | 59 | Kluge (1979) |
| Polonuevo, Los Charcos | Atlántico: CO | ICN (44414, 44415) | 10.7708 | –074.8614 | 90 | Lynch & Suárez-Mayorga (2001) |
| Soledad | Atlántico: CO | ICN (226, 227) | 10.9125 | –074.7889 | 46 | Lynch & Suárez-Mayorga (2001) |
| Puerto Colombia | Atlántico: CO | ICN (1021, 1022, 1023, 31549, 31550) | 11.0008 | –074.9500 | 18 | Lynch & Suárez-Mayorga (2001) |
| Finca Tierra Prometida; km 15, bajo | Bolívar: CO | UIS-MHN (4812) | 05.9496 | –074.4567 | 196 | BATRACHIA |
| Campo Palagua, Estación Vasconia (Ecopetrol S.A.) | Bolívar: CO | UIS-MHN (4788) | 06.0663 | –074.5567 | 148 | BATRACHIA |
| Campo Palagua, Finca San Luis | Bolívar: CO | UIS-MHN (4819–4821) | 06.0829 | –074.5650 | 133 | BATRACHIA |
| Vereda El Dique | Bolívar: CO | UIS-MHN (4805) | 06.1329 | –074.5817 | 143 | BATRACHIA |
| La Raya | Bolívar: CO | USNM (127863, 127864) | 08.3394 | –074.5389 | 34 | Kluge (1979) |
| No locality mentioned | Bolívar: CO | MHUA (7365) | 08.4162 | –074.2317 | 645 | BATRACHIA |
| Mompos | Bolívar: CO | ICN (26274, 33222) | 9.2400 | –074.4211 | 20 | Lynch & Suárez-Mayorga (2001) |
| No locality mentioned | Bolívar: CO | MHUA (0396) | 9.2411 | –074.7567 | 8 | BATRACHIA |
| Turbaco, Matute zone; 1 km N San Cristobal | Bolívar: CO | KU (15882, 15883, 15884); ICN (13727, 13728) | 9.8917 | –075.2539 | 80 | Kluge (1979); Lynch & Suárez-Mayorga (2001) |
| Santa Rosa | Bolívar: CO | ICN (2101, 2109–2121, 2248–2258, 2267–2269, 2271–2278, 2290–2302) | 10.4456 | –075.3633 | 40 | Lynch & Suárez-Mayorga (2001) |
| Santa Catalina, Hacienda El Ceibal | Bolívar: CO | ICN (44416–44461) | 10.6233 | –075.2417 | 29 | Lynch & Suárez-Mayorga (2001) |
| Vereda Las Mercedes, Los Balcones farm | Boyacá: CO | ICNMH (38047–38050, 38064) | 05.9769 | –074.5908 | 145 | Lynch & Suárez-Mayorga (2001) |
| Puerto Boyacá | Boyacá: CO | UIS-MHN (4843, 4844, 4853) | 06.0746 | –074.5567 | 142 | BATRACHIA |
| Vereda La Fiebre, La Barrilera farm | Boyacá: CO | ICNMH (38051–38053, 38066, 38067) | 9.7478 | –074.8169 | 6 | Lynch & Suárez-Mayorga (2001) |
| Vereda La Cristalina | Boyacá: CO | ICNMH (38063) | 10.3636 | –075.4172 | 130 | Lynch & Suárez-Mayorga (2001) |
| Hacienda El Valle | Caldas: CO | MHUA (5909, 5922) | 05.5913 | –074.8817 | 580 | BATRACHIA |
| No locality mentioned | Casanare: CO | ? | 06.1654 | –070.0489 | 99 | Acosta-Galvis & Alfaro (2011) |
| Vereda Morales | Cauca: CO | CD-UV (1791) | 2.9914 | –076.4069 | 1200 | Mendez-Narvaez et al. (2014) |
| El Diamante farm, 15 km S Bosconia | Cesar: CO | NS (110–117, 119–122) | 05.8419 | –074.3364 | 301 | Kluge (1979) |
| San Martin Municipality | Cesar: CO | UIS-MHN (0060) | 07.9412 | –073.6734 | 41 | BATRACHIA |
| La Gloria, Morales' swamp | Cesar: CO | ICNMH (37308, 37310) | 08.5378 | –073.7700 | 13 | Lynch & Suárez-Mayorga (2001) |
| Hacienda Montecarlo | Cesar: CO | ICNMH (37276–37280) | 08.5383 | –073.6736 | 82 | Lynch & Suárez-Mayorga (2001) |
| Simaña's swamp | Cesar: CO | ICNMH (18843) | 08.5928 | –073.7456 | 42 | Lynch & Suárez-Mayorga (2001) |
| La Jagua, 15 km S Becerril | Cesar: CO | CAS (116294) | 9.5678 | –073.2781 | 292 | Kluge (1979) |
| Socorre, upper Río Sinu | Córdoba: CO | FMNH (61168) | 07.8500 | –076.2833 | 115 | Kluge (1979) |
| Vereda Tucurá, Quebrada Lavate and Lourdes | Córdoba: CO | ICNMH (39157) | 07.9500 | –076.2833 | 103 | Lynch & Suárez-Mayorga (2001) |
| Aeropuerto El Pindo | Córdoba: CO | MHUA (3964) | 07.9829 | –075.4233 | 78 | BATRACHIA |
| Damp Urrá | Córdoba: CO | ICNMH (43401–43413) | 08.0167 | –076.2167 | 82 | Lynch & Suárez-Mayorga (2001) |
| Tierra Alta, Quebrada El Gallo | Córdoba: CO | ICNMH (39153) | 08.1061 | –076.0608 | 187 | Lynch & Suárez-Mayorga (2001) |
| Quebrada La Ron | Córdoba: CO | MHUA (3869) | 08.1719 | –076.0580 | 99 | BATRACHIA |
| Tierra Alta | Córdoba: CO | FMNH (61752); UMMZ (135336a-1) | 08.1767 | –076.0739 | 75 | Kluge (1979) |
| Catival, upper Río San Jorge | Córdoba: CO | FMNH (61169, 61170) | 08.2833 | –075.6833 | 151 | Kluge (1979) |
| Bodegas ICA | Córdoba: CO | MHUA (4496) | 08.3162 | –075.1483 | 32 | BATRACHIA |
| Montería, fish farm, Universidad Córdoba | Córdoba: CO | ICNMH (19552–19554) | 08.7472 | –075.8678 | 41 | Lynch & Suárez-Mayorga (2001) |
| Lorica | Córdoba: CO | MHUA (3540, 3541, 3550, 3551) | 9.1745 | –075.9066 | 19 | BATRACHIA |
| Bosque ITA | Córdoba: CO | ICN 48115 | 9.2661 | –075.8150 | 43 | BATRACHIA |
| Girardot | Cundinamarca: CO | AMNH (20424) | 4.3019 | –074.8044 | 324 | Kluge (1979) |
| Beltran, upper Río Magdalena | Cundinamarca: CO | USNM (152611, 152612) | 4.8003 | –074.7389 | 266 | Kluge (1979) |
| Caserio Campo Alegre | La Guajira: CO | MHUA (5604, 5605) | 10.9494 | –072.7734 | 146 | BATRACHIA |
| Finca La Necesidad | La Guajira: CO | MHUA (1131) | 10.9577 | –072.7901 | 135 | BATRACHIA |
| Rio Rancheria | La Guajira: CO | MHUA (0648, 0649, 0752, 0754) | 10.9744 | –072.7567 | 1 | BATRACHIA |
| Maicao, corregimiento Calabacito, El Cerrejón | La Guajira: CO | ICNMH (11824, 11825) | 11.0353 | –072.6589 | 140 | Lynch & Suárez-Mayorga (2001) |
| Río Barbacoa, Arroyo de Arenas | La Guajira: CO | UMMZ (54619) | 11.2717 | –072.9053 | 47 | Kluge (1979) |

*Continued*

**Appendix, Table A1.** *Continued.*

| Locality | State: country | Voucher | Latitude | Longitude | Elevation (m a.s.l.) | Source |
|---|---|---|---|---|---|---|
| Corregimiento Botillero | Magdalena: CO | UIS-MHN (837, 671–682, 684, 686–768, 770, 830–836, 838–848, 874, 875, 877, 889–894, 960, 1277–1294, 1575–1578, 1938–1941) | 9.0995 | –073.9817 | 103 | BATRACHIA |
| Curumani | Magdalena: CO | MCZ (21475–21479, 21483) | 9.2011 | –072.5425 | 50 | Kluge (1979) |
| Casco Urbano | Magdalena: CO | MHUA (0771) | 9.2411 | –074.3483 | 25 | BATRACHIA |
| Guamal Municipality; | Magdalena: CO | MHUA(3903) | 9.2495 | –074.2317 | 22 | BATRACHIA |
| Becerril | Magdalena: CO | CAS (116280) | 9.7036 | –073.2789 | 138 | Kluge (1979) |
| Plato | Magdalena: CO | AMNH (71042) | 9.7911 | –074.7975 | 6 | Kluge (1979) |
| Fundación | Magdalena: CO | UMMZ (46908–46912, 46914–46921) | 10.5089 | –074.1822 | 67 | Kluge (1979) |
| Aracataca | Magdalena: CO | ANSP (19779) | 10.5914 | –074.1861 | 42 | Kluge (1979) |
| Minca | Magdalena: CO | ICNMH (3863) | 11.1428 | –074.1075 | 1530 | Lynch & Suárez-Mayorga (2001) |
| No locality mentioned | Magdalena: CO | UIS-MHN (0459) | 11.2327 | –073.7150 | 239 | BATRACHIA |
| El Aranar farm, nr. Bonda | Magdalena: CO | USNM (152715, 152716) | 11.2458 | –072.1233 | 45 | Kluge (1979) |
| Puerto Gaitan, Vereda San Miguel, Fundación Yamato | Meta: CO | ICNMHN (38283) | 4.2810 | –072.0705 | 151 | Lynch & Suárez-Mayorga (2001) |
| Nearness airport Camilo Daza, Cúcuta | Norte de Santander: CO | Uncatalogued | 07.9311 | –072.5125 | 308 | Armesto et al. (2009) |
| Astillero, old town | Norte de Santander: CO | ICNMH (33554–33557) | 08.1197 | –072.5783 | 140 | Lynch & Suárez-Mayorga (2001) |
| Landázuri, Hacienda Las Flores | Santander: CO | ICNMH (8796) | 06.1367 | –073.8811 | 685 | Lynch & Suárez-Mayorga (2001) |
| Hacienda San Miguel, ciénaga de Cachimbero | Santander: CO | MHUA (2818) | 06.3829 | –074.3317 | 127 | BATRACHIA |
| Hacienda Bufalera El Bosque, Campamento El Encanto | Santander: CO | MHUA (3640, 2628, 3185–3201, 3641–3698) | 06.4662 | –074.3400 | 109 | BATRACHIA |
| Planta Sebastopol | Santander: CO | UIS-MHN (5124) | 06.4746 | –074.3900 | 71 | BATRACHIA |
| Vélez, Carare zone, Campo Capote | Santander: CO | ICNMH (613–615) | 06.6192 | –073.9147 | 139 | Lynch & Suárez-Mayorga (2001) |
| Finca La Olinda | Santander: CO | MHUA (1917) | 06.6496 | –074.0567 | 83 | BATRACHIA |
| Doradas | Santander: CO | UIS-MHN (0006) | 06.8912 | –073.5484 | 172 | BATRACHIA |
| San Vicente | Santander: CO | ANDES-A (1207, 1453, 1541) | 06.8953 | –073.4303 | 535 | Guarnizo et al. (2015) |
| El Centro | Santander: CO | AMNH (71043) | 06.9358 | –073.7514 | 93 | Kluge (1979) |
| Vereda Marta | Santander: CO | UIS-MHN (4187, 4187) | 07.1162 | –073.4234 | 279 | BATRACHIA |
| Cerro La Aurora | Santander: CO | UIS-MHN (3577, 3579) | 07.1746 | –073.3234 | 618 | BATRACHIA |
| Sabana de Torres Municipality | Santander: CO | ANDES-A (1533, 1538–1540) | 07.3547 | –073.4900 | 145 | Guarnizo et al. (2015) |
| Sabana de Torres Municipality | Santander: CO | UIS-MHN (0515, 0570, 0571) | 07.3745 | –073.5984 | 118 | BATRACHIA |
| Vereda Agua Bonita, Reserva Natural El Cabildo Verde, puesto de control 1 | Santander: CO | UIS-MHN (3857) | 07.3745 | –073.4984 | 141 | BATRACHIA |
| No locality mentioned | Santander: CO | UIS-MHN (3524) | 07.4995 | –073.7734 | 42 | BATRACHIA |
| San Marcos, station Crocodilia | Sucre: CO | IAvH (5337, 5703) | 08.5453 | –075.1833 | 46 | Lynch & Suárez-Mayorga (2001) |
| San Marcos | Sucre: CO | IAvH (6668, 6669) | 08.6578 | –075.1316 | 36 | BATRACHIA |
| Vereda La Caimanera, Sector de la Caimanera | Sucre: CO | IAvH (8235, 8214, 8279, 8215–8218, 8238, 8239, 8243, 8276, 8280) | 9.4495 | –074.9067 | 52 | BATRACHIA |
| Colosó, Proyecto Primates | Sucre: CO | IAvH (1167) | 9.4950 | –075.3528 | 140 | Lynch & Suárez-Mayorga (2001) |
| Hacienda La Estanzuela, 4 km E Tolu | Sucre: CO | NS (42, 43, 240–243) | 9.5225 | –075.5833 | 3 | Kluge (1979) |
| Vereda El Sereno Bajo, 1 km al sur de la Estación Primatológica | Sucre: CO | IAvH (8081, 8086, 8156–8158, 8170) | 9.5245 | –075.3566 | 192 | BATRACHIA |
| Vereda El Sereno Alto, Quebrada El Sereno, arriba de la estación | Sucre: CO | IAvH (8062, 8113) | 9.5328 | –075.3566 | 192 | BATRACHIA |
| Vereda Macajan, Hacienda Mundo Nuevo | Sucre: CO | IAvH (8360, 8362, 8336, 8363, 8375, 8359, 8374) | 9.5745 | –075.4483 | 26 | BATRACHIA |
| San Luis de Onofre [San Onofre] | Sucre: CO | ICNMH (42289) | 9.7400 | –075.5203 | 43 | Lynch & Suárez-Mayorga (2001) |
| Espinal, Magdalena Valley | Tolima: CO | MCZ (15063, 15064) | 4.1483 | –074.8844 | 333 | Kluge (1979) |
| Honda | Tolima: CO | USNM (152121, 152122, 156888) | 05.2050 | –074.7364 | 173 | Kluge (1979) |
| Bitaco, near, on way to Dagua | Valle del Cauca: CO | USNM (151982) | 3.5906 | –076.6413 | 1426 | USNMW |
| Municipality of La Victoria | Valle del Cauca: CO | CD-UV (1792) | 4.4772 | –076.0454 | 940 | Mendez-Narvaez et al. (2014) |
| Las Tablas | Los Santos: PA | CHP:Herp (0020) | 07.7655 | -80.2706 | 37 | CHPW |
| Guanico, Arriba Río Guanico | Los Santos: PA | KU (116361) | 07.3406 | -80.4961 | 87 | Kluge (1979) |
| Tonosi | Los Santos: PA | KU (101553–101555) | 07.3872 | -80.4667 | 70 | Kluge (1979) |
| Bejuco, Río Bejuco | Panama: PA | AMNH (69766) | 08.5733 | –079.8842 | 35 | Kluge (1979) |
| Proyecto Los Islotes, near Los Islotes de Quebro. | Veraguas: PA | CHP:Herp (8501) | 07.4014 | -80.9231 | 0 | CHPW |

*Continued*

**Appendix, Table A1.** *Continued.*

| Locality | State: country | Voucher | Latitude | Longitude | Elevation (m a.s.l.) | Source |
|---|---|---|---|---|---|---|
| La Florida, 45 km W Coro | Falcón: VE | CIEZAH (401) | 11.2333 | –070.0667 | 152 | Mijares-Urrutia & Arends (1999) |
| Bridge on the Chama river, near El Vigía | Mérida: VE | ULABG (5671–5675) | 08.6097 | –071.6397 | 183 | This study |
| 3.5 km W desvío a Caja Seca | Mérida: VE | ULABG (3292) | 9.1208 | –071.0567 | 320 | La Marca (1996) |
| Nearness Arapuey, Sur del Lago de Maracaibo | Mérida: VE | MHNLS (20914–20917) | 9.2833 | –071.0167 | 57 | This study |
| Brisas del Chama, 3 km from El Vigía to Caja Seca, just next the bridge | Mérida: VE | ULABG (5711–5713) | 08.6133 | –071.6247 | 170 | This study |
| Aprox. 10 km El Vigía, border between Mérida and Zulia | Mérida: VE | ULABG (5319) | 08.6979 | –071.6931 | 104 | This study |
| Finca Santa Lucía, road El Vigía-El Quince | Mérida: VE | ULABG (4100) | 08.5935 | –071.7502 | 149 | This study |
| Near to Guayabones, 22 km NE de El Vigía | Mérida: VE | CVULA (141) | 08.7508 | –071.5732 | 154 | This study |
| Las Virtudes | Mérida: VE | ULABG (1587) | 9.1293 | –070.9745 | 605 | This study |
| Sector Vera de Agua, 10 km de El Vigía, road to Sta. Bárbara | Mérida: VE | ULABG (5318, 5320) | 08.7119 | –071.6992 | 95 | This study |
| Agropecuaria San Sebastián; Machiques de Perijá | Zulia: VE | MBLUZ (?) | 9.8676 | –072.3996 | 100 | Infante-Rivero & Velozo (2015) |